UNIVERSITÉ DU QUÉBEC À MONTRÉAL

L'INTERPRÉTATION DE LA SÉLECTION D'HABITAT COMME MÉCANISME DE COEXISTENCE CHEZ UNE COMMUNAUTÉ DE SCIURIDÉ VIA LE COMPORTEMENT D'APPROVISIONNEMENT

MÉMOIRE

PRÉSENTÉ

COMME EXIGENCE PARTIELLE

DE LA MAÎTRISE EN BIOLOGIE

PAR

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AVANT-PROPOS

Ce mémoire est présenté en trois sections incluant une introduction générale, la présentation de l'étude sous forme d'article (rédigée en anglais dans la perspective d'une soumission à une revue scientifique) et en dernier lieu, une conclusion générale qui placera l'étude dans un contexte plus large.

Les objectifs principaux de cette étude étaient la validation du modèle de Rieucau et al. (2009) et son application subséquente afin d'estimer la préférence d'habitat en plus de l'efficience d'approvisionnement des espèces dans un but plus général d'évaluer la sélection d'habitat comme mécanisme de coexistence. Le modèle (Rieucau et al. 2009) a été utilisé pour la première fois chez une communauté de sciuridés afin d'évaluer la perception des espèces vis-à-vis la qualité de leurs habitat par rapport aux différents coûts d'alimentation.

L'étude s'est déroulée sur une période de 5 mois, de la mi-mai à la mi-octobre 2013. Bien que l'étude devait en principe terminer à la fin août, la prise de données a été allongée due à l'insuffisance d'activités auprès des écureuils et des tamias à plusieurs périodes au courant de l'été.

Le design expérimental initial incluait une période d'enrichissement à l'aide de parcelles artificielles (mangeoires de nourriture) dans la forêt de feuillus et dans la plantation de noyers noirs afin de faire la validation du modèle de Rieucau et al. (2009). Cependant, l'ajout de nourriture était insuffisante et on a eu recours à un enrichissement naturel dans la plantation de noyers (après la fructification) pour vérifier les inférences du modèle.

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RÉSUMÉ

La sélection d'habitat peut agir comme mécanisme favorisant la coexistence selon deux axes : les espèces peuvent différer dans leur perception de la qualité d'habitat selon les coûts d'approvisionnement (coûts de prédation, métaboliques et d'opportunités manquées) et/ou dans leur efficience d'approvisionnement dans différents habitats. Ces deux éléments peuvent être évalués via le comportement d'approvisionnement en mesurant la quantité de nourriture abandonnée par un animal lorsque celui-ci quitte une parcelle de nourriture (Giving-up density; GUD). Les inférences d'un modèle utilisant une méthode de supplémentation mis au point par Rieucau et al. (2009) ont été utilisées afin de séparer et identifier les coûts d'approvisionnement responsables pour ces différences dans le comportement d'approvisionnement. L'objectif de cette étude vise à mesurer la quantité de nourriture abandonnée afin de 1) vérifier la validité du modèle de Rieucau et al. (2009) et 2) d'inférer des informations sur la perception des coûts et sur l'efficience d'approvisionnement des espèces associés à un habitat afin d'évaluer la sélection d'habitat comme mécanisme de coexistence chez une communauté de Sciuridés. L'étude s'est déroulée à l'Arboretum Morgan à Sainte-Anne-de-Bellevue, Québec où l'écureuil gris (*Sciurus carolinensis*), l'écureuil roux (*Tamiasciurus hudsonicus*) et le tamia rayé (*Tamias striatus*) coexistent dans trois habitats distincts (forêt conifériennе, forêt de feuillus et plantation de noyers). L'utilisation de mangeoires filmées a permis l'identification de l'espèce ayant laissé la plus petite quantité de nourriture. Les animaux ont réagi à l'enrichissement du milieu selon les inférences du modèle de Rieucau et al. (2009) le validant ainsi et permettant son utilisation pour le deuxième volet de l'étude. Les résultats démontrent que les tamias rayés perçoivent une abondance de nourriture plus élevée mais aussi un plus grand risque de prédation dans la forêt de feuillus. Les écureuils gris perçoivent la plantation de noyers comme étant la plus pauvre en nourriture. L'écureuil gris était toujours la ou l'une des espèces avec la plus grande efficience d'exploitation dans les trois habitats. Par contre, l'efficience relative de l'écureuil gris et du tamia et leur activité d'approvisionnement dans les mangeoires diffèrent conjointement dans le temps suggérant qu'un compromis temporel plutôt que spatial favoriserait davantage la coexistence des espèces.

Mots-Clés : coûts d'approvisionnement · théorie d'approvisionnement optimal · giving-up density (GUD) · qualité d'habitat · coexistence

INTRODUCTION GÉNÉRALE

Idéalement, les décisions pour la conservation de la biodiversité devraient être effectuées au niveau de l'écosystème plutôt qu'au niveau d'espèces par espèces. Ainsi, l'utilisation d'une plus grande unité écologique, telle que la communauté, a plus de chance de prendre en compte les diverses interactions entre les espèces (Morris et al. 2009). De ce fait, il est particulièrement intéressant de déterminer les caractéristiques du milieu et des organismes qui permettent aux espèces de coexister. La coexistence peut être expliquée par des mécanismes qui produisent des inégalités dans les niches écologiques entre les espèces (Brown 1989). Un de ces mécanismes est la sélection d'habitat qui a lieu lorsqu'il y a une utilisation non aléatoire de l'habitat par les individus. Cette utilisation non aléatoire de l'habitat peut être dû à 1) l'hétérogénéité de l'environnement perçu différemment par les espèces en terme de coûts d'approvisionnement (les coûts associés aux risques de prédation, les coûts énergétiques ainsi que les coûts d'opportunités manquées) et/ou à 2) un compromis évolutif telle qu'une différence d'efficience d'approvisionnement entre les espèces.

La sélection de l'habitat a lieu lorsqu'il y a une utilisation non aléatoire de l'habitat par les individus. La différence en sélection de l'habitat entre les espèces peut faciliter leur coexistence. Malgré le fait que plusieurs méthodes d'évaluation de la sélection d'habitat existent (Morris et al. 2009), elles ne sont pas toujours adéquates. Parmi ces méthodes, l'utilisation des fonctions de la sélection de ressources (RSF) constitue une façon de décrire l'utilisation des ressources dans l'habitat par rapport à leurs disponibilités. Cette méthode a le problème d'être purement descriptive et de ne pas considérer la valeur de l'habitat (Morris et al.

2009). Une seconde méthode est celle des isodars, un concept proposé par Morris (1987). Les isodars sont une extension des fonctions de la sélection de ressources (RSF) qui prennent en compte la densité d'une population permettant une analyse plus complexe. Cependant, cette méthode est rarement utile lorsqu'on veut évaluer la sélection de l'habitat dans un contexte interspécifique car les isodars ne prennent en compte ni l'influence de la compétition entre les espèces (Morris et al. 2009) ni la perception des animaux envers leur environnement.

L'étude du comportement alimentaire est une méthode d'estimation de la sélection d'habitat qui permet d'évaluer la perception des coûts ainsi que l'efficience d'approvisionnement. En milieu naturel, la distribution des ressources alimentaires a tendance à être répartie de façon contagieuse dans l'environnement. Un individu qui s'alimente dans une parcelle de nourriture voit son rendement d'approvisionnement diminuer dans le temps, c'est-à-dire que la nourriture devient de plus en plus difficile à trouver à mesure qu'elle est consommée. Selon la théorie d'approvisionnement optimal, un animal devrait quitter une parcelle de nourriture lorsque son taux d'approvisionnement n'excède plus les coûts d'approvisionnement (Charnov 1976, Brown 1988). La quantité de nourriture abandonnée par l'animal lorsque celui quitte une parcelle de nourriture (Giving-up density; GUD) permet d'estimer le taux d'approvisionnement où l'animal juge que les coûts et les bénéfices d'approvisionnement sont égaux (Brown 1988). Si on compare le comportent d'approvisionnement d'une espèce dans plusieurs habitats, un GUD élevé est un signe de coûts d'approvisionnement élevés. Par exemple, l'animal laissera une grande quantité de nourriture (GUD élevé) s'il perçoit un grand risque de prédation, un coût métabolique élevé et/ou un coût d'opportunités manquées élevé dans son habitat. À l'aide d'un modèle mathématique basé sur un système de supplémentation développé par Rieucau et al. (2000), il est maintenant possible

d'isoler le ou les coûts d'approvisionnement responsables du changement de comportement de l'animal afin de faire des inférences sur leur préférence d'habitat. Le GUD permet également d'interpréter l'efficience relative de plusieurs espèces à l'intérieur d'un même habitat. Une espèce est plus efficiente qu'une autre si elle est capable de réduire davantage la quantité de nourriture laissée dans la parcelle (GUD plus faible).

L'étude présentée vise à évaluer si la sélection d'habitat constitue un mécanisme favorisant la coexistence dans une communauté de sciuridés composée de l'écureuil roux (*Tamiasciurus hudsonicus*), de l'écureuil gris (*Sciurus carolinensis*) et du tamia (*Tamias striatus*). Ces trois espèces sont diurnes et possèdent une alimentation semblable (Woods 1980). Le tamia rayé et l'écureuil roux sont tous les deux territoriaux tandis que l'écureuil gris est plutôt social (Woods 1980). Le tamia à tendance à faire des réserves en centralisant sa nourriture (Giraldeau and Kramer 1982) et entre en hibernation durant l'hiver tandis que les écureuils demeurent actifs (Woods 1980). L'écureuil roux a aussi tendance à faire des réserves mais elles sont souvent plus dispersées (Woods 1980).

L'écureuil roux possède une préférence pour les forêts de pins et de sapins où il peut s'alimenter de graines des cônes de conifères, une ressource préférée faisant parti de sa diète (Woods 1980, Steele 1998, Holloway et Malcolm 2006). À l'inverse, la littérature propose que l'écureuil gris et le tamia rayé semblent préférer les forêts de feuillus (Koprowski 1994b, Snyder 1982).

Des études antérieures sur ses mêmes espèces suggèrent que la variation temporelle des ressources et la sélection de l'habitat ont possiblement un effet conjoint favorisant leur coexistence. Guerra et Vickery (1998) et Saropoulos (1996)

ont proposé que l'effet de l'habitat seul ne permet pas d'expliquer la coexistence des espèces de Sciuridés. Néanmoins, ils ont trouvé une interaction espèce-habitat hautement significative. Il serait donc intéressant de décrire cette différence d'efficience et de perception des espèces entre les habitats et de suggérer comment elle peut promouvoir la coexistence de ces espèces.

La sélection d'habitat peut favoriser la coexistence si chacune des espèces possède un habitat qu'elle perçoit de meilleure qualité (selon les coûts d'approvisionnement) et/ou si elle possède un habitat où elle est la plus efficiente. Plus précisément, les principaux objectifs du projet comportent les deux volets suivants : Le premier volet consiste à valider le modèle basé sur un système de supplémentation pour la communauté de sciuridés à l'étude en enrichissant le milieu. Le deuxième volet consiste à l'emploi du modèle pour interpréter la perception des coûts d'approvisionnement ainsi que d'estimer l'efficience relative d'approvisionnement des espèces dans différents habitats.

Nous prévoyons qu'une des raisons expliquant la coexistence de certaines espèces avec des niches écologiques généralement semblables réside dans la différence entre leur perception des coûts d'alimentation dans différents habitats et dans leur différence d'efficacité d'approvisionnement dans ces habitats. Ainsi, nous tentons d'étudier l'importance relative de la prédation et de l'abondance de nourriture afin de tirer des inférences sur la préférence d'habitat.

L'étude s'est déroulée à l'Arboretum Morgan à Sainte-Anne-de-Bellevue, Québec où les trois espèces de Sciuridés sont actifs de la fin du printemps jusqu'à l'automne. Trois habitats distincts (une forêt coniférienne, une forêt de feuillus ainsi qu'une plantation de noyers noirs) de 100 m^2 ont été délimité à l'intérieure de l'arboretum

(Figure 1.1). Chacune des trois espèces ont été observés dans les trois types de forêts qui étaient séparés d'au moins 200 m afin d'éviter qu'un même individu visite plus d'un habitat. Chaque habitat de 100 m^2 a été divisé en 100 quadrats de 10 m^2 où 12 quadrats ont été sélectionnés aléatoirement. Dans les quadrats sélectionnés, des parcelles artificielles de nourriture ont été créées en installant au sol de la forêt des mangeoires remplis de sable (2L) avec 100 ou 200 graines de tournesols. À la fin d'une période d'une heure, les mangeoires étaient triés et le nombre de graines restantes était compté (GUD). Chacune des mangeoires était filmées à l'aide d'un caméscope. Cette méthode est plus précise pour l'attribution du GUD à l'espèce que par l'identification de traces ou par la manipulation d'écailles de graines utilisées antérieurement (Peschard 2003). Le problème avec ces deux dernières méthodes est qu'il est difficile d'attribuer avec confiance le GUD à une espèce particulière si plusieurs espèces ont visité la parcelle de nourriture préalablement. L'utilisation de caméscopes fera en sorte qu'il y aura beaucoup moins d'ambiguïté face à l'identification de la dernière espèce qui s'est approvisionnée dans une parcelle donnée et permet également une identification encore plus précise, soit d'identifier l'individu.

Jusqu'à présent, les GUDs ont souvent été mesuré pour l'évaluation de qualité d'habitat chez les Sciuridés (Saropoulos 1996, Guerra et Vickery 1998, Whelan et Jedlicka 2007, Wheeler et Hik 2014). Cependant, il était impossible de séparer l'effet de chacun des coûts d'alimentation. En validant le modèle de Rieucau et al. (2009), celui-ci pourra alors être utilisé comme outil d'estimation de qualité d'habitat plus précis que les méthodes utilisées auparavant. Ainsi, l'utilisation du modèle permettra pour la première fois d'examiner en détail le rôle de la sélection d'habitat par rapport à l'importance relative du risque de prédation et de l'abondance de nourriture selon la perception des espèces de Sciuridés dans leur habitat. Si le

modèle s'avère valable, il pourrait aussi être utilisé pour évaluer la préférence d'habitat de certaines espèces afin de développer des recommandations dans un contexte de conservation.

Figure 1.1 Map of GUD collection sites at the Morgan Arboretum in Sainte-Anne-de-Bellevue, Quebec (45° 30'N, 73° 36' W). Blue dots: stations in the black walnut plantation; red dots: stations in deciduous forest; yellow dots: stations in coniferous forest. Image courtesy of Google Earth.

ARTICLE À SOUMETTRE: USING FORAGING BEHAVIOUR AND HABITAT SELECTION TO EVALUATE COEXISTENCE IN A COMMUNITY OF SCIURIDS

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ABSTRACT

Coexistence can be explained by mechanisms that recognize inequalities in niches between species. One of these mechanisms is habitat selection where species can differ in their perception of habitat quality in terms of foraging costs (predation risks, metabolic costs and missed opportunity costs) and foraging efficiency in different habitats. These two elements can be evaluated via foraging behaviour by measuring the quantity of food abandoned by an animal when it leaves a food patch (giving-up density; GUD). A low GUD is an indication of superior foraging efficiency. However, when one considers how a species perceives different habitats, a high GUD may be associated with a high predation risk, high energy cost or abundant food. The inferences of a model using a method of supplementation developed by Rieucau et al. (2009) are used to separate and identify the costs responsible for the higher GUD. The main objective of this study is to measure the quantity of abandoned food to 1) verify the validity of Rieucau et al.'s (2009) model and 2) to infer the perception of habitat quality in terms of costs and the foraging efficiency of species to evaluate if habitat selection would be a potential mechanism favoring coexistence in a community of Sciurids. The study took place at the Morgan Arboretum in Sainte-Anne-de-Bellevue, Québec where the grey squirrel (*Sciurus carolinensis*), red squirrel (*Tamiasciurus hudsonicus*) and the Eastern chipmunk (*Tamias striatus*) coexist in three distinct habitats (a coniferous forest, a deciduous forest and a black walnut plantation respectively). Feeders were filmed using camcorders to identify the last individual/species to forage. The results show that animals reacted to a natural enrichment of the environment according to the inferences of the Rieucau et al. (2009) model and thus allowing its use for the second component of the study. Results demonstrate that grey squirrels perceive the walnut plantation as the habitat with less food whereas chipmunks perceive a higher abundance of food but also a greater risk of predation in the deciduous forest. Despite the fact that red squirrels almost only fed in feeders from the coniferous forest, they were the least efficient of the three species in terms of foraging in this habitat. The grey squirrel was always the (or one of the) most efficient foragers in all three habitats. However, the relative foraging efficiency of the grey squirrel and the chipmunk, as well as their activity in feeders, both differed temporally suggesting that a temporal trade-off might be more important than a spatial compromise (i.e. habitat selection) in favouring the coexistence of these species.

Keywords: foraging costs · optimal foraging theory · giving-up density (GUD) · habitat quality · coexistence

INTRODUCTION

In principle, management and conservation efforts should be focused at a community level rather than being species specific. According to Morris et al. (2009), the more conservation goals are developed from individual species, the more there are chances of conflicts between conservation efforts. Thus, the use of a larger ecological unit such as a community has a greater chance of taking into account species interactions and of conserving multiple species. Consequently, identifying the main characteristics of organisms and the environment that allow species coexistence would be of particular interest for conservation biology. Species coexistence can be explained by mechanisms that recognize inequalities in ecological niches between species on two axes. The first is environmental heterogeneity which causes species to use resources differently and the second is the evolutionary trade-offs where species' efficiencies differ for different tasks (Brown 1989, Morris et al. 2009). The combination of the two axes can allow species to coexist when each outcompetes the other for different resources, in different habitats or at different times (Brown 1989). The mechanisms by which species coexist may be revealed via the animal's behaviour when it is foraging in food patches (Brown 1988; Kotler et al. 2007; Baker and Brown 2012).

Habitat selection as a mechanism of coexistence

Habitat selection occurs when there is a non-random use of the habitat by individuals. Differences in habitat selection between species may facilitate coexistence. Several methods to evaluate habitat selection exist but they are not always adequate (Morris et al. 2009). Among these available methods, the resource

selection function (RSF) is a way to describe resource use in the habitat compared to its availability. The problem with this method is that it is purely descriptive and does not consider all aspects of the habitat. Ideally, RSFs should include fitness-density maps but these types of studies need to be carried out over long periods to allow for multiple generations (Morris et al. 2009). A second method is the use of isodars, a concept proposed by Morris (1987). Isodars are extensions of RSFs that take population density into account thus allowing a more complex analysis. However, this method is rarely useful when we want to assess habitat selection at an interspecific level because isodars do not account for the influence of competition between species (Morris et al. 2009) nor the animals' perception of their environment in terms of costs. On the other hand, the animal's foraging behaviour reveals information on its perception of the habitat in which it forages. We can directly apply the principles of the optimal foraging theory in order to interpret the behaviour (Brown 1988).

Optimal patch-use model using food supplementation

Optimal foraging theory assumes that animals make decisions that maximize their food intake (Charnov 1976, Brown 1988). In a natural environment, resources tend to have a contagious distribution. An individual who finds and feeds in a food patch sees its harvesting success decrease over time, meaning that food becomes increasingly hard to find as it is consumed (Charnov, 1976). The individual must constantly evaluate the costs and benefits of remaining or leaving to search for another food patch. Charnov's (1976) marginal value theorem for optimal foraging supposes that an individual foraging in a given food patch obtains an energetic gain linked directly to fitness. The model proposes that the consumer should leave the

food patch when the marginal harvest rate of the patch becomes less than that of the habitat. Decisions taken by animals while they are foraging are in fact clues to their perception of the associated costs of foraging (missed opportunity costs, metabolic costs and predation costs) which can be experimentally manipulated. Brown (1988) developed a model based on Charnov's (1976) work in order to include these foraging costs. The giving-up density (GUD) is the density (or quantity) of food left in a food patch when an individual ceases to forage there. A higher GUD may indicate either a high abundance of food (signifying a habitat of good quality), or a high-risk of predation and/or a high metabolic cost (poor quality).

Rieucau et al. (2009) developed an optimal patch-use model based on a system of food supplementation to separate the effects of foraging costs. Thus, the model reveals not only the animal's perception of relative habitat quality but also the reason for which the habitat is perceived in such a way (which costs are involved). The model is based on Brown's (1992) optimal quitting harvest rate model. The GUD_i (equation 1) is produced at the foraging rate, f_i, at which an individual should leave patch i when benefits no longer exceed foraging costs divided by the encounter rate with food, a_i, when it is optimal for the individual to leave the patch to search for food elsewhere. The instantaneous risk of predation is defined by μ and Φ is the rate at which opportunities are lost (missed opportunity cost) while c_i corresponds to the energetic cost of foraging in patch i. The probability of surviving is represented by p whereas reproductive success (increase in fitness) per unit of food consumed is represented by $\partial F/\partial e$ where F is the expected number of descendants as a result of the quantity of food consumed following a given strategy.

$$\text{GUD}_i = f_i/a_i = \left(\frac{\mu(F+1)}{\partial F/\partial e} + \frac{\Phi}{p\partial F/\partial e} + c_i\right)\Big/ a_i \quad (1)$$

We consider missed opportunity to be the cost of not being able to feed elsewhere in the habitat while in a given food patch. This cost increases with the abundance of food in the habitat. By adding a richer food patch near the initial patch, it is possible to increase missed opportunity costs and thus distinguish them from other costs. While predation risk and metabolic costs remain the same for two foragers feeding in two feeders that are side by side, missed opportunity costs will differ. The individual foraging in the initial patch will have a higher missed opportunity cost than if it were foraging in the enriched patch since the perceived abundance of food in the surrounding area includes the food in the enriched patch in addition to the food already present in the habitat (Rieucau et al. 2009).

Two different models formulated by Rieucau et al. (2009) can be applied depending on spatial foraging tactics. In the first model, two habitat types are considered being part of the same environment if both are exploited by the same individuals (when individuals can move freely from one habitat to another). When this is the case, the model comparing habitat quality within an environment should be used. However, if individuals always remain and forage in a given habitat type without ever traveling to the other one, the second model comparing habitat quality between environments should be used. The reason why there are two models is because Olsson and Molokwu (2007) suggested that individuals that are able to move freely between habitats would not perceive costs the same way as individuals who are limited to only one habitat type.

Model comparing habitat quality within an environment

Whereas GUD_i corresponds to the GUD left behind at station i when only a single feeder (the initial feeder) is available, equation 2 illustrates the GUD of the individual who is foraging in the initial feeder (GUD_i^X) when there is a richer feeder beside it. *X* represents the addition of food in the richer feeder whereas *m* is proportional to the animal's perception of the food already present in the environment. To compare the quality of habitats (or microhabitats) within an environment, we use equation 3 to calculate the difference in GUDs (ΔGUDs) with and without the presence of the supplemental (i.e. richer) feeder (Rieucau et al. 2009).

$$GUD_i^X = \left(\frac{\mu(F+1)}{\partial F^X/\partial e} + \frac{\Phi + X/m}{p\partial F^x/\partial e} + c_i \right) \Big/ a_i \qquad (2)$$

$$\Delta GUD_i = GUD_i^X - GUD_i = \frac{X}{a_i m p \partial F^x/\partial e} + \frac{\left(\delta F/\delta e - \delta F^x/\delta e\right)}{a_i \delta F/\delta e \, \delta F^x/\delta e} \times \left(\mu_i(F+1) + \frac{\emptyset}{p}\right) \qquad (3)$$

In equation 3, missed opportunity costs and predation risk can be separated since both costs have opposing effects on ΔGUD. If predation risk and food encounter rates are fixed characteristics of the habitat, then clearly risky environments will produce higher ΔGUD than habitats which are rich in food. However, in order to reduce its instantaneous predation risk, μ_i, an animal may modify its food encounter rate, and thus also a_i, by slowing down its foraging rate to be more vigilant. Therefore, a decline in a_i, when μ_i is high will generate a high GUD as well as a high ΔGUD (Scenario 5, Table 1.1). In contrast, if abundant food is more important, the animal should keep foraging at the same high rate and therefore have a greater food encounter rate than if predation risk was the important cost, thus producing a lower

ΔGUD (Scenario 2, Table 1.1). In equation 3, the overall survival probabilities when using a given foraging strategy, p, and the overall rate at which opportunities are lost, Φ, remains constant since they are environmental parameters and are not specific to habitat.

If there is no difference between ΔGUDs, the habitat with the largest GUD may have both a high predation risk and a high abundance of food or the habitat could have a relatively higher metabolic cost (Scenario 4, Table 1.1). However, when there is no difference between GUDs, the habitat with the lowest ΔGUD is considered of highest quality because it indicates rich resource abundance through a high food encounter rate and a low risk of predation (Scenario 1, Table 1.1).

Model comparing habitat quality between environments

To compare between habitats, we first measure the giving-up density when only the main initial feeder is present (GUD_i). Subsequently, we measure the ΓGUD (equation 5), which is the difference between the GUD of the richer supplemental feeder (GUD_i^S; equation 4) and the initial feeder (GUD_i^X; equation 2) when both feeders are placed next to each other as developed by Rieucau et al. (2009).

$$GUD_i^S = \left(\frac{\mu(F+1)}{\partial F^X/_{\partial e}} + \frac{\Phi + bX/m}{p\partial F^x/_{\partial e}} + c_i \right) \Big/ a_i \qquad (4)$$

$$\Gamma GUD_i = GUD_i^S - GUD_i^X = X\left(a_i - \frac{1-b}{mp\partial F^x/_{\partial e}} \right) \qquad (5)$$

If p is the overall probability of surviving, then $1\text{-}p$ is the overall probability of being killed or predated (as a result of high predation risk or in extreme cases, high

metabolic costs) while using a given strategy and should be constant within an environment but might differ when comparing between environments. Therefore, we can distinguish the effects of predation (*1-p*) from the effects of missed opportunity costs (via the animal's perception of food available elsewhere in the environment, *m*) since they have opposite effects on ΓGUD. Abundant food, expressed through a large *m*, will produce a greater difference in GUDs between the two feeders (larger ΓGUDs) whereas low survival probabilities (*p*) because of high predation risk will generate lower ΓGUDs.

If abundant food (high missed opportunity cost) is responsible for high GUDs, then there should be a greater difference in GUDs between the two feeders (larger ΓGUDs) (Scenario 2, Table 1.2). If there is no difference in GUDs between habitats, the habitat with the largest ΓGUD (Scenario 1, Table 1.2) is considered of highest quality because it indicates a rich abundance of resource and a low risk of predation (or low metabolic costs). However, if GUDs differ but the ΓGUDs are similar between habitats, abundant food as well as high predation risk or metabolic costs are responsible for high GUDs (Scenario 4, Table 1.2).

Table 1.1 Inferences about the relative quality of habitat 1 compared to habitat 2 in terms of foraging costs when the same individual can sample both habitats (2 habitats within the same environment) according to the Rieucau et al. (2009) optimal foraging model using supplementation. GUD_1 represents the giving-up density in habitat 1 whereas GUD_2 represents the giving-up density in habitat 2. The scenarios are numbered in order of highest to lowest relative quality.

	$GUD_1 = GUD_2$	$GUD_1 > GUD_2$
$\Delta GUD_1 < \Delta GUD_2$	SCENARIO 1 Habitat 1: ↓ Predation cost and ↑ Food encounter rate	SCENARIO 2 Habitat 1: ↑ Food encounter rate
$\Delta GUD_1 = \Delta GUD_2$	SCENARIO 3 Habitat 1: Habitat quality equivalent to habitat 2	SCENARIO 4 Habitat 1: ↑ Metabolic cost or ↑ Food encounter rate and ↑ predation cost
$\Delta GUD_1 > \Delta GUD_2$	SCENARIO 6 Habitat 1: ↑Predation cost and ↓ Food encounter rate	SCENARIO 5 Habitat 1: ↑ Predation cost

Table 1.2 Inferences about the relative quality of habitat 1 compared to habitat 2 in terms of foraging costs when a given individual cannot sample both habitats (2 habitats in different environments) according to the Rieucau et al. (2009) optimal foraging model using supplementation. GUD_1 represents the giving-up density in habitat 1 whereas GUD_2 represents the giving-up density in habitat 2. The scenarios are numbered in order from highest to lowest relative quality.

	$GUD_1 = GUD_2$	$GUD_1 > GUD_2$
$\Gamma GUD_1 > \Gamma GUD_2$	SCENARIO 1 Habitat 1: ↑Food abundance and ↓ Predation cost or metabolic cost	SCENARIO 2 Habitat 1: ↑ Food abundance
$\Gamma GUD_1 = \Gamma GUD_2$	SCENARIO 3 Habitat 1: Habitat quality equivalent to habitat 2	SCENARIO 4 Habitat 1: ↑ Food abundance and ↑ Predation cost or metabolic cost
$\Gamma GUD_1 < \Gamma GUD_2$	SCENARIO 6 Habitat 1: ↓ Food abundance and ↑ Predation cost or metabolic cost	SCENARIO 5 Habitat 1 : ↑ Predation cost

Objectives

Sciurids are often studied using GUDs (Brown 1988; Morgan and Brown 1996; Guerra and Vickery 1998; Thorson et al. 1998; Kotler et al. 1999). Three species of Sciuridaes, the grey squirrel (*Sciurus carolinensis*), red squirrel (*Tamiasciurus hudsonicus*), and Eastern chipmunk (*Tamias striatus*), coexist within the Morgan Arboretum at Sainte-Anne-de-Bellevue, Québec. These species are diurnal and have a similar diet (Woods 1980) but most importantly, they cohabit in different habitat types.

This study aims to assess whether habitat selection is a mechanism favoring coexistence among the studied community of sciurids. Habitat selection can favour coexistence if each species has a preferred habitat in terms of foraging costs or if it has a habitat where it is the most efficient forager. The main objectives of the project include the following two components:

1. Validation of Rieucau et al.'s (2009) optimal patch use model to compare habitat quality

First we validate the optimal patch-use model based on a system of supplementation. Although the white-tailed deer's responses (Vickery et al. 2011) were in accordance with the inferences from Rieucau et al.'s (2009) patch use model, the validity of the model has not yet been tested. Vickery et al. (2011) suggested that the validity of the model could be tested by comparing the model's interpretation of GUDs with measures of fitness. However, methods to measure reproductive success in order to estimate fitness are challenging and time consuming because it implies calculating the ratio of juveniles per adult. Another potential approach to test the validity of the model is to modify one foraging cost

while keeping the others constant to see if the animals respond in accordance with the model's predictions.

The black walnut plantation was naturally enriched when fruiting occurred at the end of August. For this reason, we profited from the naturally occurring food supplementation to test if animals reacted according to the model's inferences. The grey squirrel has been shown to favour black walnuts (Koprowski 1994) so this natural resource supplement should be reflected by the giving-up density of our artificial food patches. *T. striatus,* however, should not react to the food supplement because walnuts are not a profitable food for them because of the large size of the nut and the hardness of the husk (Guerra et Vickery 1998). We assume that fruiting does not have consequences for predation risk. If the model applies, we predict that GUDs and ΓGUDs for grey squirrels should be higher following fruiting of the black walnuts as suggested in SCENARIO 2 (Table 1.1) while the eastern chipmunk's foraging behaviour should not be affected (SCENARIO 3; Table 1.1)

2. Evaluating habitat selection as a mechanism of coexistence

The evaluation of habitat selection is two-fold. Habitat selection may favour coexistence in this community if: 1) each species has a preferred habitat that it perceives as better quality and/or 2) each species has a distinctive habitat where its foraging efficiency is higher than other species. The first part concerns habitat preferences and requires using Rieucau et al.'s (2009) optimal patch use model to determine how the different sciurid species perceive their habitat in terms of foraging costs. Subsequently, we need to determine the relative foraging efficiency of animals in each habitat to see if there is a trade-off between species.

METHODS

Study site

Fieldwork was conducted from early May to mid-October 2013 at the Morgan Arboretum in Sainte-Anne-de-Bellevue, Quebec (45° 30'N, 73° 36' W) where the grey squirrel (*Sciurus carolinensis*), the red squirrel (*Tamiasciurus hudsonicus*) and the eastern chipmunk (*Tamias striatus*) co-occur. Three distinct habitat types, each of 10 000 m^2, separated by at least 200 m were delimited within the arboretum. The first was a coniferous forest, specifically a white spruce (*Picea glauca*) plantation. In addition to white spruce (the dominant tree species), eastern larch (*Larix laricina*) and immature sugar maple (*Acer saccharum)* were also common. The second habitat was a naturally occurring deciduous forest where the most common species were sugar maple (*Acer saccharum)* and American beech (*Fagus grandifolia*). The third habitat that we studied was a black walnut *(Juglans nigra*) plantation where American Linden (*Tilia americana*), American Ash (*Franxinus americana*) and sugar maple (*Acer saccharum*) were also commonly present. All three sciurid species were observed in each of the delimited habitats. These three studied forest types are naturally existing habitats for the three sciurid species.

Experimental design

Each habitat was partitioned into 100 quadrats of 100 m^2 (10 m by 10 m) with 12 of these quadrats (hereafter stations) being randomly selected for the placement of artificial food patches (hereafter feeders). In order to avoid a habitat-enriching effect from other feeders, the 12 stations were divided into 4 groups of 3 stations to maximize the minimum distance between active feeders. At any given time, only

three stations were sampled per habitat following a rotation for the four groups. At each station we counted the number of large (dbh > 10cm) and small trees (dbh < 10cm) for each species. We estimated forest vegetation cover (by calculating total vegetation area using Image J) and ground cover (proportion of floor vegetation and logs using a line-transect method). Feeders were centered on the ground in each station and consisted of round plastic trays (radius = 23 cm) with 100 or 200 shelled sunflower seeds mixed with a 2 L sand matrix. Shelled sunflower seeds were selected as the food source because a previous study (Tremblay 2000) showed that there was no difference in foraging efficiencies for this food type among the three sciurids and that there was a general preference for sunflower seeds with the shells compared to those without.

Prior to data collection, there was a period of capture and marking (by fur cuttings in the shape of numbers on the hip of the animals) for individual identification. This allowed us to see if an individual would visit more than one habitat during the study in order to select the appropriate model (within or between environments).

Our experimental design comprised two treatments that were temporally separated by 2-3 weeks. The first treatment involved placing a single feeder (initial feeder) containing 100 seeds (Fig 1.2a) whereas the second treatment involved adding a second feeder (supplementary feeder) containing twice as many seeds (200) next to the initial one of 100 seeds by a distance of ≈ 0.5 meter (Fig 1.2b). The same two treatments were set up in an enriched habitat (Fig 1.2b and 1.2c) which was the naturally enriched walnut plantation after fruiting in order to validate Rieucau et al.'s model (2009).

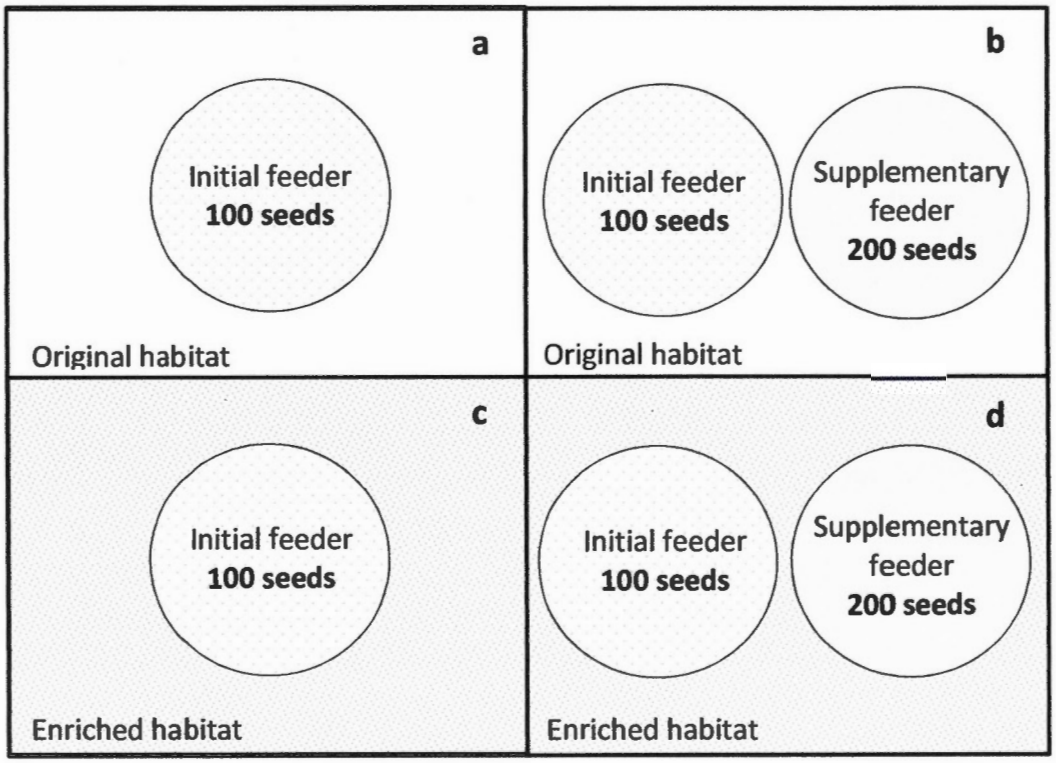

Figure 1.2 Layout of feeders at a station according to the different treatments **(a, b, c, d)**. Feeders are placed on the ground and centered at each station. ΓGUD is the difference in GUDs between the supplementary feeder and the initial feeder in treatment **(b)**. ΔGUD is the difference in GUDs between the initial feeder in treatment **(b)** and the initial feeder in treatment **(a)**. Treatment **(c)** and **(d)** were set up at stations in the walnut plantation after fruiting exclusively (enriched habitat) in order to validate Rieucau et al.'s model (2009).

A camcorder (Vide digital camera 5.0) recorded the feeders for a period of one hour (between 8:00am and 6:00pm on days without precipitation). If tracks were present in feeders at the end of a trial, the number of seeds left (GUD) was counted and the ambient temperature at the feeder was recorded. If an animal was still foraging in the feeder or if we scared the animal away on our arrival, we discarded the trial.

Statistical analyses

We performed linear mixed models with partially crossed random effects using R (R Core Team, 2014) and the package lme4 (Bates et al. 2014) to analyse GUDs in relation to our two objectives. For all analyses, both variables "identity of individuals" and "stations" were treated as random effects as Barr et al. (2013) recommended including the maximum random effects justified by the design. Although stations were selected randomly in each habitat, microhabitat effects at each station might influence mean giving-up density, thus creating interdependencies. Fixed effects factors included species, habitats, weeks, temperature, floor cover data (% vegetation and % logs), number of large trees (dbh > 10cm), and number of small trees (dbh < 10cm). Since vegetation cover was strongly correlated with number of trees, the variable was omitted from the models.

All GUDs were log transformed in order to improve normality and homoscedasticity. Models were selected using Akaike's Information Criterion (AIC) based on ordinary likelihood (REML=false) since we were only interested in comparing models which differed in their fixed effect variables. Models with the lowest AICs were retained (Akaike 1974, Burnham and Anderson 2002). In addition, within each model, we kept variables that were identified as significant ($p<0.05$) by the ANOVA component of a stepwise algorithm (argument = step).

RESULTS

A total of 441 GUDs were recorded in 2035 one-hour trials from July to mid-October 2013. Although red squirrels were observed in all three habitats, they were seen only once foraging in feeders in the deciduous forest and twice in the black walnut plantation. For this reason, only their GUDs from the coniferous forest were considered in the following analyses.

Model validation: S. carolinensis

First, GUDs and ΓGUDs were analyzed before and after fruiting (enriched habitat) in the black walnut plantation to test the validity of the Rieucau et al. (2009) optimal foraging model using supplementation. For *S. carolinensis*, the model best describing GUDs and the model best describing the difference in GUDs when two feeders were present (ΓGUDs) both contained fruiting state (before and after food supplementation) as the only factor (Table 1.3). Grey squirrels left more food behind (higher GUDs) and a higher difference in GUDs between two feeders (higher ΓGUDs) when the plantation was naturally enriched with walnuts (Fig 1.3). GUDs and ΓGUDs were highest after fruiting; suggesting, based on our model (Scenario 2, see Table 1.2), that missed opportunity cost is the main influence.

Model validation: T. striatus

The model best describing the GUDs for *T. striatus* included temperature and the number of small trees (dbh < 10 cm) in the 10x10m transects (Table 1.4). The model

best describing the difference in GUDs when two feeders were present (ΓGUDs) similarly contained number of small trees but also included the percentage of logs (Table 1.4).

GUDs and ΓGUDs did not differ before and after fruiting as fruiting state was not included in the best fit model, indicating that *T. striatus* did not respond to the food augmentation (Fig 1.3) perceiving resource state as constant between the two periods in terms of foraging costs (Scenario 3, see Table 1.2).

Table 1.3 Linear mixed effect models best predicting GUDs (log transformed) and ΓGUDs for *S. carolinensis* in the black walnut plantation before and after fructification using Akaike criteria (AIC). All models include both stations and individuals as random effect factors. Fixed effect variables include: fs = fruiting state (before vs after); temp = temperature; lg_trees = number of large trees (dbh > 10 cm); sm_trees = number of small trees (dbh < 10 cm); veg = percentage of ground vegetation and logs = percentage of logs. All other models have larger AIC values (> 156.58 for GUDs and > 357.92 for ΓGUDs).

GUD (n=55)		ΓGUD (n=34)	
Model	AIC	Model	AIC
fs*	152.65	fs*	354.44
fs* + temp	153.74	fs* + sm_trees	355.04
fs* + lg_trees	153.75	fs* + lg_trees	355.82
fs* + sm_trees	154.58	fs* + logs	355.94
fs* + veg	154.63	fs* + veg	356.24
fs* + logs	154.63	fs* + temp	356.4
fs* + temp + lg_trees	154.96	fs* + trees + sm_trees	356.56
fs* + lg_trees + logs	155.56	fs* + sm_trees + logs	356.89
fs* + temp + sm_trees	155.65	fs* + temp + sm_trees	357
fs* + temp + logs	155.73	fs* + temp + lg_trees	357.8
fs* + sm_trees + logs	156.58	fs* + veg + logs	357.92

*Significant variables in model (p<.05)

Table 1.4 Linear mixed effect models best predicting GUDs (log transformed) and ΓGUDs for *T. striatus* in the black walnut plantation before and after fructification using Akaike criteria (AIC). All models include both stations and individuals as random effect factors. Fixed effect variables include: fs = fruiting state (before vs after); temp = temperature; lg_trees = number of large trees (dbh > 10 cm); sm_trees = number of small trees (dbh < 10 cm); veg = percentage of ground vegetation and logs = percentage of logs. All other possible models have larger AIC values (> 240.54 for GUDs and > 427.96 for ΓGUDs).

GUD (n=115)		ΓGUD (n=41)	
Model	AIC	Model	AIC
temp + sm_trees*	237.96	sm_trees* + logs	424.59
fs + sm_trees*	238.96	temp + sm_trees* + logs	425.23
temp + lg_trees + sm_trees*	239.13	sm_trees*	426.42
fs + temp + sm_trees*	239.27	fs + sm_trees* + logs	426.43
temp + sm_trees* + logs	239.45	sm_trees* +veg + logs	426.58
sm_trees*	239.75	lg_trees + sm_trees* + logs	426.59
temp + sm_trees* + veg	239.94	fs + temp + sm_trees* + logs	426.67
temp + lg_trees + sm_trees* + veg	240.33	temp + lg_trees + sm_trees* + logs	427.15
fs + lg_trees + sm_trees*	240.41	temp + sm_trees* + veg + logs	427.21
temp	240.5	temp + sm_trees*	427.39
fs + temp* + lg_trees + sm_trees*	240.54	sm_trees* + veg	427.96

*Significant variables in model (p<.05)

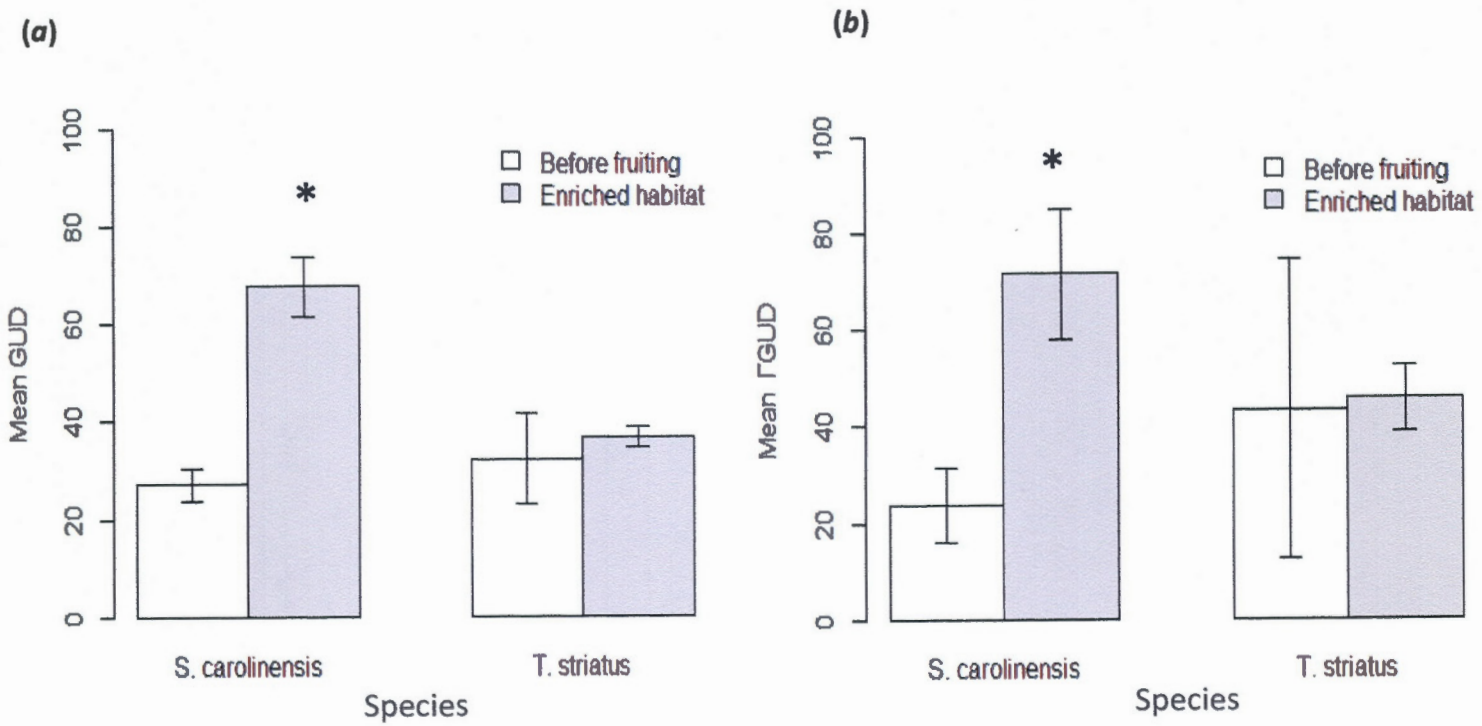

Figure 1.3 **(*a*)** Mean GUD (±SE) and **(*b*)** mean difference in GUD between two feeders (main feeder = 100 sunflower seeds and supplementary feeder = 200 seeds) placed side by side (ΓGUD ± SE) for *S. carolinensis* and *T. striatus* in the black walnut plantation (*Juglans Nigra*) before and after fruiting (naturally causing habitat resource enrichment). Asterisks (*) represent significant differences ($p<0.05$) using a stepwise ANOVA.

Habitat quality: S. carolinensis

The patch use model comparing habitat quality within an environment was the one used for grey squirrels as a result of videos showing that individuals from this species foraged in more than one habitat. The model which best described GUDs for *S. carolinensis* when the initial feeder is the only feeder present included the variables habitat, week, number of small trees (dbh < 10 cm) and percentage of ground vegetation (Table 1.5). The model which best described ΔGUDs (the difference in GUDs in the initial feeder with and without the presence of a supplementary feeder) included supplementation (present or absent), habitat, week, number of small trees (dbh < 10 cm) and the interaction between supplementation and habitat (Table 1.5). GUDs were highest whereas ΔGUDs were lowest in the coniferous and deciduous forest compared to the black walnut plantation (Fig 1.4). According to the inferences from Rieucau et al. (2009) model, the coniferous and deciduous forests have a higher missed opportunity cost than the black walnut plantation (Scenario 2, see Table 1.1).

Habitat quality: T. striatus

The model which best described GUDs for *T. striatus* included the variable week (AIC = 340.64). However, the second best model differing by an AIC value of 0.15 (AIC = 340.79) includes the variable habitat in addition to week. A stepwise regression of the model revealed that although adding habitat did not improve the model's overall AIC value, the parameter <habitat> was indeed significant ($p < 0.05$) and was therefore retained in the model (Table 1.6). The model best describing ΓGUD for *T. striatus* included the variables small trees and logs (Table 1.6). *T. striatus* individuals left higher GUDs in the deciduous forest and the lowest GUDs in the coniferous

forest (Fig 1.5a) whereas there was no difference in ΓGUDs between habitats (Fig 1.5b). This suggests that missed opportunity costs as well as the predation cost are higher for the habitats in the following order: deciduous forest > black walnut plantation > coniferous forest (Scenario 4, see Table 1.2).

Species efficiencies

The model best describing GUDs in the coniferous forest includes the variables trees and species (Table 1.7). *S. carolinensis* and *T. striatus* left significantly lower GUDs (indicating a higher foraging efficiency) than *T. hudsonicus* (Fig 1.6). In the deciduous forest, the model best describing GUDs included species, week and temperature (Table 1.8). *S. carolinensis* left significantly lower GUDs than *T. striatus* (Fig 1.6). The model best describing GUDs in the black walnut plantation included week, temperature, number of trees and vegetation (Table 1.9). However, the difference in AICs with the model containing species was only 0.9 and a stepwise algorithm indicated species as a significant variable in the model suggesting that *S. carolinensis* was significantly more efficient in terms of foraging in the walnut plantation (Fig 1.6). *S. carolinensis* was generally the more efficient forager leaving the lowest GUD followed by *T. striatus* when only the main feeder was present (Fig 1.7; Table 10).

The best model describing the totality of GUDs when only the main feeder was present includes species, week and the interaction between the two (Table 1.10). The variable habitat only appears in the third best model, suggesting that species and week are more important in describing GUDs. *S. carolinensis* left significantly lower GUDs in the first part of the study period (July-August) while *T. striatus* left the lowest GUDs in the second half of the study from September to mid-October (Fig 1.8a). In addition, *S. carolinensis* had a higher foraging activity in the artificial food

patches (visited more feeders) earlier in the study while *T. striatus* was more active in the second half (Fig 1.8b).

Table 1.5 Linear mixed effect models best predicting GUDs (log transformed) and ΔGUDs (log transformed) and ΓGUDs for for *S. carolinensis* using Akaike criteria (AIC). All models include both stations and individuals as random effect factors. Fixed effect variables include: sup = supplementary feeder (present or absent); hab = habitat; week = week number (1-15); temp = temperature; lg_trees = number of large trees (dbh > 10 cm); sm_trees = number of small trees (dbh < 10 cm veg = percentage of ground vegetation and logs = percentage of logs. All other possible models have larger AIC values (> 142.63 for GUDs and > 386.78 for ΔGUDs).

GUD (n=54)		ΔGUD (n=168)	
Model	AIC	Model	AIC
hab + week* + sm_trees* + veg	138.97	sup* + hab + week* + sm_trees + sup × hab	382.89
hab + week* + sm_trees*	39.03	sup* + hab + week* + sup × hab	383.51
hab + week* + temp + sm_trees*	140.33	Sup* + hab + week* + sm_trees	384.46
hab + week* + temp + sm_trees* + veg	140.5	sup*+ week* + lg_trees*	384.63
hab + week* + sm_trees* + veg + logs	140.97	sup* + hab + week*	384.93
hab + week* + sm_trees* + logs	140.98	sup* + hab + week* + temp + sm_trees	386.09
hab + week* + lg_trees + sm_trees*	141.02	sup* + week* + temp + lg_trees*+ sm_trees	386.11
week* + sm_trees*	142.06	sup* + hab + week* + temp	386.38
hab + week* + lg_trees + veg	142.29	sup* + week* + sm_trees*	386.4
hab + week* + temp + sm_trees* + veg + logs	142.5	sup* + hab + week* + lg_trees	386.7
week* + temp + sm_trees*	142.63	sup *+ hab + week* + logs	386.78

*Significant variables in model (p<.05)

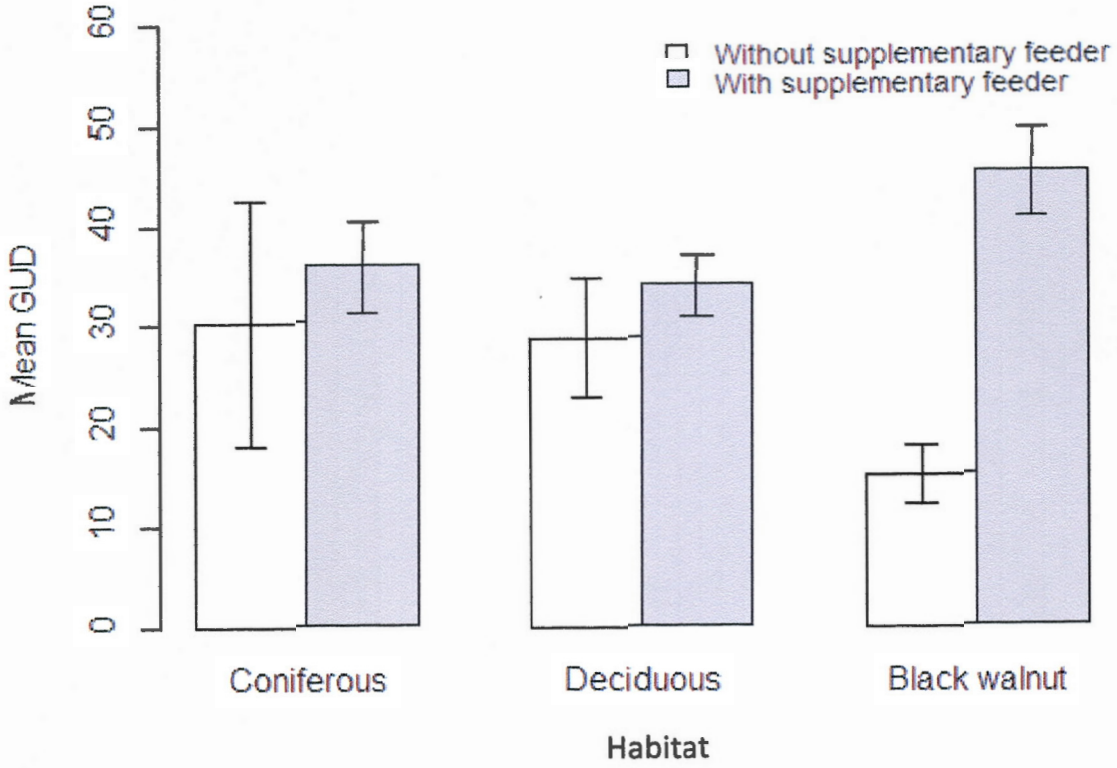

Figure 1.4 Mean GUD (±SE) left by *S. carolinensis* in main feeders (initial number of seeds = 100) without and with the presence of a supplementary feeder for three different habitats (coniferous forest, deciduous forest and black walnut plantation). The difference between GUDs in the main feeders with and without the presence of a supplementary feeder represents ΔGUD.

Table 1.6 Linear mixed effect models best predicting GUDs (log transformed) and ΓGUDs (log transformed) for *T. striatus* using Akaike criteria (AIC). All models include both stations and individuals as random effect factors. Fixed effect variables include: hab = habitat; week = week number (1-15); temp = temperature; lg_trees = number of large trees (dbh > 10 cm); sm_trees = number of small trees (dbh < 10 cm); veg = percentage of ground vegetation and logs = percentage of logs. All other possible models have larger AIC values (> 342.74 for GUDs and > 753.39 for ΓGUDs).

GUD (n=144)		ΓGUD (n=73)	
Model	AIC	Model	AIC
week*	340.64	sm_trees* + logs*	750.12
hab* + week*	340.79	temp + sm_trees* + logs*	750.94
week* + temp	341.21	logs*	750.97
hab* + week* + temp	341.85	sm_trees* + veg + logs*	751.3
week* + veg	342.12	temp + logs*	751.76
hab + week* + lg_trees	342.46	lg_trees + sm_trees* + logs*	752.07
hab* + week* + logs	342.5	temp + sm_trees* + veg + logs*	752.37
week* + lg_ trees	342.53	veg + logs*	752.39
week* + sm_trees	342.62	lg_trees + sm_trees* + veg + logs*	752.86
week* + logs	342.63	lg_trees + logs*	752.95
hab + week* + veg	342.74	veg + logs*	753.39

*Significant variables in model (p<.05)

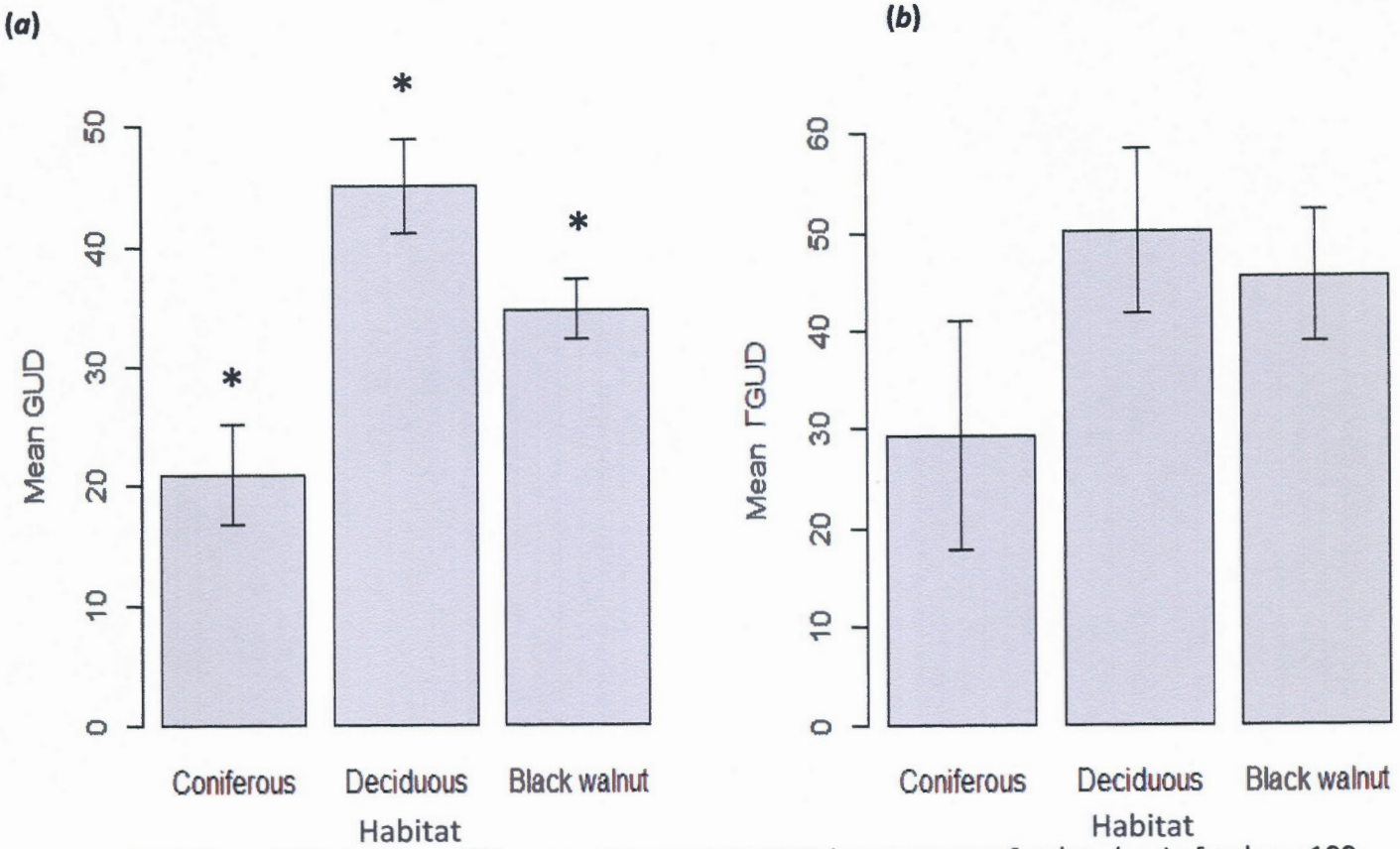

Figure 1.5 **(*a*)** Mean GUD (±SE) and **(*b*)** mean difference in GUD between two feeders (main feeder = 100 sunflower seeds and supplementary feeder = 200 seeds) placed side by side (ΓGUD ±SE) for *T. striatus* in three different habitats (coniferous forest, deciduous forest and black walnut plantation). Asterisks (*) represent significant differences ($p<0.05$) using a stepwise ANOVA.

Table 1.7 Linear mixed effect models best predicting GUDs (log transformed) in the deciduous forest using Akaike criteria (AIC) for the three species of sciurids. All models include both stations and individuals as random effect factors. Fixed effect variables include: sp = species; week = week number (1-15); temp = temperature; lg_trees = number of large trees (dbh > 10 cm); sm_trees = number of small trees (dbh < 10 cm); veg = percentage of ground vegetation and logs = percentage of logs. All other possible models have larger AIC values (> 395.15).

Deciduous forest (GUD; n=75)	
Model	AIC
sp* + week* + temp*	389.23
sp* + week* + temp* + veg	390.95
sp* + week* + temp* + logs	391.02
week* + temp*	391.12
week* + temp* + sm_trees	392.72
sp* + week* + temp* + veg + logs	392.77
sp* + week* + temp* + lg_trees + logs	392.89
week* + temp* + veg	392.97
week*	394.51
sp* + week* + temp* + lg_trees + veg + logs	394.68
sp* + week* + sm_trees + veg	395.15

*Significant variables in model (p<.05)

Table 1.8 Linear mixed effect models best predicting GUDs (log transformed) in the coniferous forest using Akaike criteria (AIC). All models include both stations and individuals as random effect factors. Fixed effect variables include: sp = species; week = week number (1-15); temp = temperature; lg_trees = number of large trees (dbh > 10 cm); sm_trees = number of small trees (dbh < 10 cm); veg = percentage of ground vegetation and logs = percentage of logs. All other possible models have larger AIC values (> 138.3).

Coniferous forest (GUD; n=58)	
Model	AIC
sp* + lg_trees*	132.68
sp* + week + lg_trees*	133.06
sp* + temp + lg_trees*	133.89
sp* + week + lg_trees* + sp×week	134.18
sp* + week + temp + lg_trees*	134.98
sp* + week + lg_trees* + sm_trees + logs + sp×week	136.33
sp*	136.66
sp* + week	137.34
sp* + sm_trees	137.93
sp* + week + sp×week	138.05
sp* + temp	138.2

*Significant variables in model (p<.05)

Table 1.9 Linear mixed effect models best predicting GUDs (log transformed) in the black walnut plantation using Akaike criteria (AIC). All models include both stations and individuals as random effect factors. Fixed effect variables include: sp = species; week = week number (1-15); temp = temperature; lg_trees = number of large trees (dbh > 10 cm); sm_trees = number of small trees (dbh < 10 cm); veg = percentage of ground vegetation and logs = percentage of logs. All other possible models have larger AIC values (> 223.35).

Black walnut plantation (GUD; n=97)	
Model	AIC
week* + temp + lg_trees + veg*	221.66
week* + temp + veg	221.94
week* + temp	222.26
week* + lg_trees + veg*	222.3
week* + veg	222.53
sp* + week* + sp×week	222.56
week* + temp + sm_trees + veg	222.86
sp* + week* + temp + sp×week	222.89
week*	222.92
week* + sm_trees + veg	223.16
sp* + week* + temp + lg_trees + veg*	223.35

*Significant variables in model (p<.05)

Figure 1.6 Mean GUD (±SE) for *S. carolinensis*, *T. striatus* and *T. hudsonicus* in three different habitats (coniferous forest, deciduous forest and black walnut plantation). *T. hudsonicus* data were omitted in the two last habitats due to small sample size ($n \leq 2$). Asterisks (*) represent significant differences ($p<0.05$) using a stepwise ANOVA.

Table 1.10 Linear mixed effect models best predicting GUDs (log transformed) when only the main feeder is present using Akaike criteria (AIC). All models include both stations and individuals as random effect factors. Fixed effect variables include: habitat= habitat type; sp = species; week = week number (1-15); temp = temperature; lg_trees = number of large trees (dbh > 10 cm); sm_trees = number of small trees (dbh < 10 cm); veg = percentage of ground vegetation and logs = percentage of logs. All other possible models have larger AIC values (> 553.74).

Deciduous forest (GUD; n=230)	
Model	AIC
sp* + week* + sp × week*	550.65
sp* + week* + small_trees + sp × week*	551.8
habitat* + sp* + week* + sp × week*	552.51
sp* + week* + lg_trees + sp × week*	552.57
sp* + week* + veg + sp × week*	552.64
sp* + week* + temp + sp × week*	552.65
habitat* + sp* + week* +lg_ trees + sp × week*	553.41
sp* + week* + small_trees + logs + sp × week*	553.48
habitat* + sp* + week* + small_trees + sp × week*	553.65
sp* + week* + lg_trees + small_trees + sp × week*	553.71
sp* + week* + small_trees + veg + sp × week*	553.74

*Significant variables in model (p<.05)

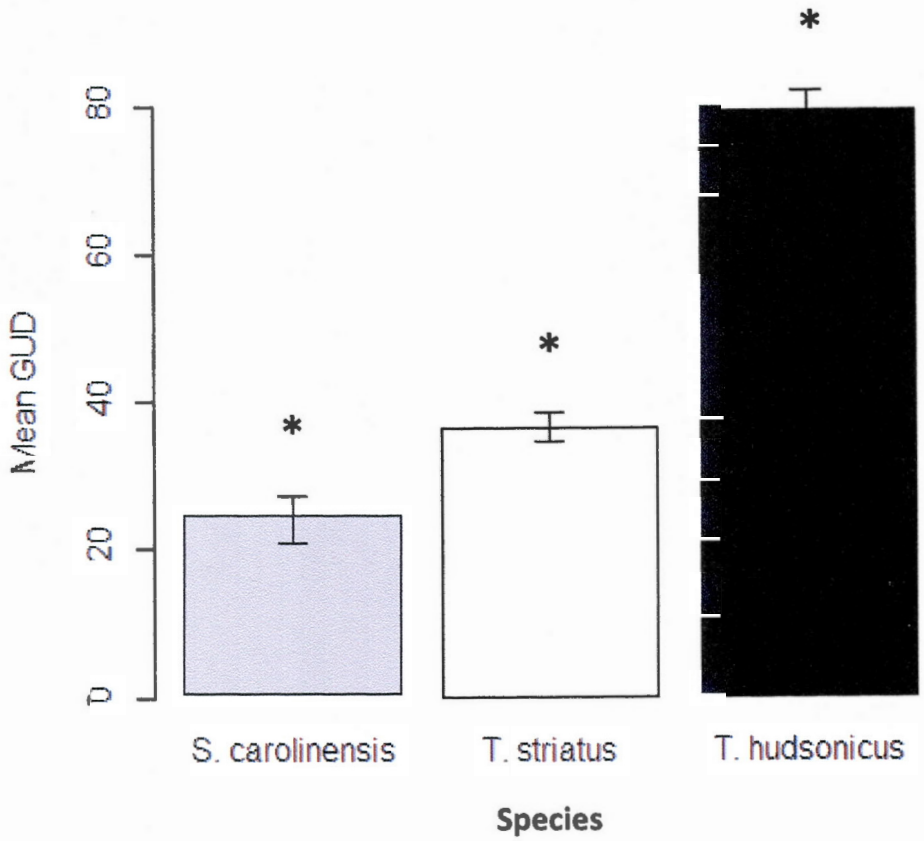

Figure 1.7 Mean GUD (±SE) for *S. carolinensis*, *T. striatus* and *T. hudsonicus* when only the main feeder is present. Asterisks (*) represent significant differences ($p<0.05$) using a stepwise ANOVA.

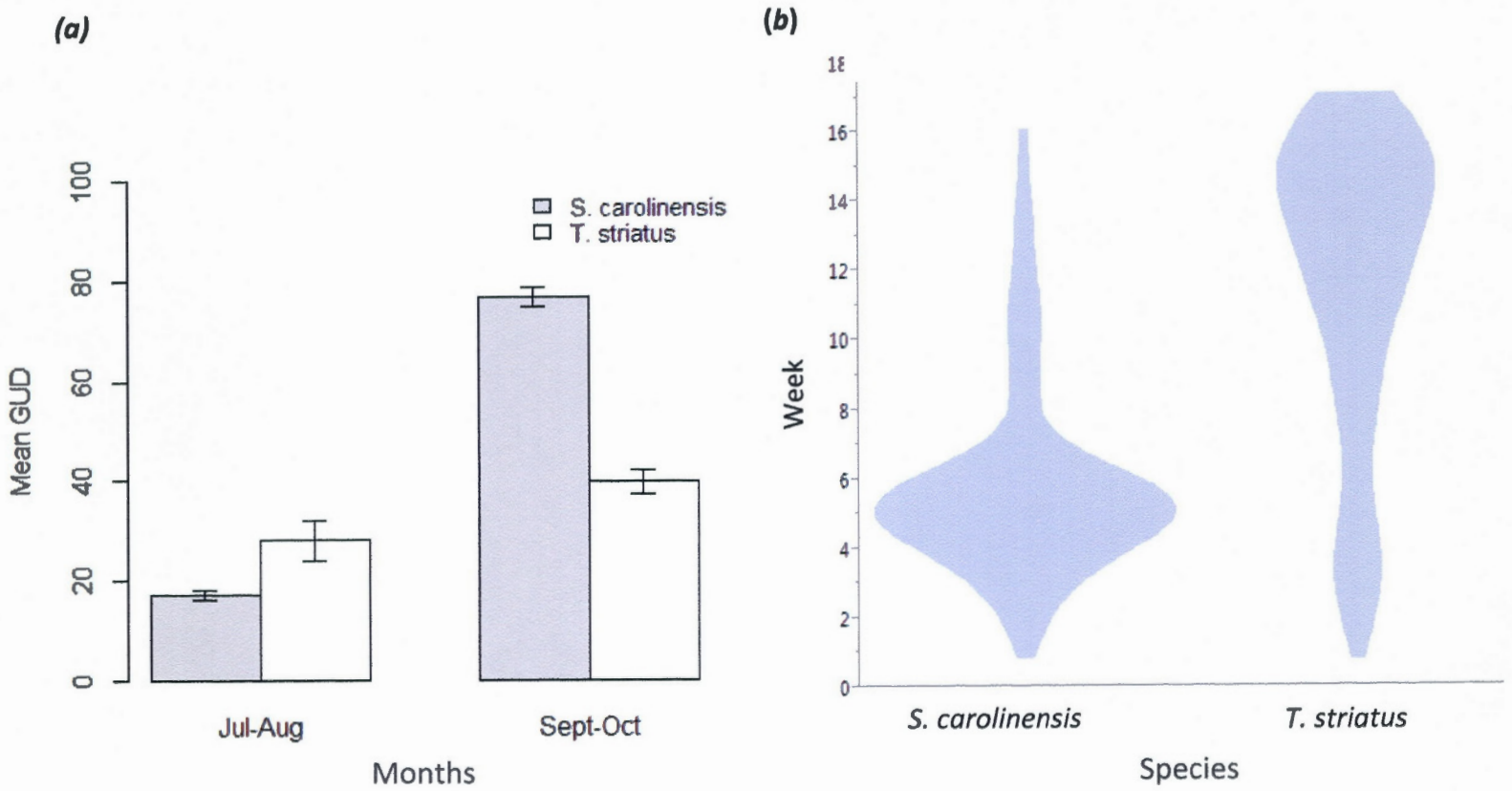

Figure 1.8 **(*a*)** Mean GUD (±SE) for *S. carolinensis* and *T. striatus* in the first half (July-August) and second half (September-October) of data collection of the field study. **(*b*)** Width represents the proportion of visits in feeders by species per week (week 1 being the first week of the study) for *S. carolinensis* and *T. striatus*.

DISCUSSION

After validating the effectiveness of the optimal patch-use model developed by Rieucau et al. (2009) comparing habitat quality between environments, we were able to use it to test for habitat preferences of our study species. Our results demonstrate that animals react to changes in their habitat (changes in walnut fruit abundance) by optimally changing their foraging behaviour according to the optimal patch-use model (Rieucau et al. 2009). The main factor influencing GUDs and ΓGUDs for *S. carolinensis* was walnut availability (before and after fruiting of walnuts) while the main factor influencing GUDs and ΓGUDs for *T. striatus* appeared to be the number of small trees (dbh < 10cm). *T. striatus* left lower GUDs in areas with more small trees suggesting they perceived lower predation risk in more covered microhabitats. The fact that *T. striatus* did not perceive a food increase in the habitat makes sense and is in accordance with the model's prediction since walnut fruits are not profitable to *T. striatus* because of their size and the hardness of the husk (Guerra et Vickery 1998). By knowing that our study species' responses are in line with those predicted by Rieucau et al. (2009), we can make robust inferences regarding each species' perception of its habitat quality.

Habitat quality

Predation risk is usually assumed to be the primary foraging cost responsible for differences in GUDs (Brown and Kotler 2004). However, Olsson and Molokwu (2007) proposed that missed opportunity costs could be as important when the comparison is between environments. Our results from the mixed models suggest that both predation risk and food abundance are responsible for variations in GUDs for the eastern chipmunks. They perceive the relative quality of the deciduous forest

associated with the highest food abundance but also with the highest predation risk. This is possible because high food abundance may attract more individuals, which in turn, may attract more predators (Olsson & Molokwu 2007). Chipmunks perceived the coniferous forest, which had the highest average density of trees (dbh > 10cm), as less risky. This is surprising because we would expect smaller animals such as chipmunks to be more sensitive to lower story shelter (ground vegetation and small bushes). Although no significant differences in ΓGUDs between habitats were detected, the pattern in figure 1.5b is consistent with an effect due to food abundance only (habitat with the highest GUD seems to also have the highest ΓGUD). This pattern supports Olsson and Molokwu's idea that food abundance can indeed affect GUDs and also show the value of the Rieucau et al. (2009) model.

Habitat preference for *S. carolinensis* was treated in a model comparing habitat quality within an environment (using GUDs and ΔGUDs) since some individuals were observed foraging in more than one habitat (specifically, the deciduous forest and black walnut plantation). This led us to suppose that they would estimate missed feeding as the average cost of not feeding across the habitats, as proposed by Olsson and Molokwu (2007). However, the model by Rieucau et al. (2009) suggests that through food encounter rate, animals may perceive differences in food abundance between two habitats within the same environment. Our results reflect this as the walnut plantation was the habitat associated with lowest food encounter rate, thus suggesting that they perceived this habitat with the least food. However, grey squirrels were mostly observed in the walnut plantation possibly indicating that this is the habitat where they live. We obtained few GUDs from grey squirrels when walnuts were very abundant late in the season. Thus, our results mainly reflect the squirrels' perception of the habitat early in the summer prior to fruiting indicating a poor habitat where it would be advantageous to extend travel to sample other

habitats. We hypothesize that grey squirrels inhabit the walnut plantation because they anticipate greater food abundance at a later date. This was an experimental study and the three habitat studied are specific to the Morgan Arboretum. We are not generalising our findings to other habitats of the same forest types elsewhere.

Our results impact Olsson and Molokwu's (2007) approach to estimating habitat quality. For example, Olsson and Molokwu's (2007) were able to theoretically demonstrate that within an animal's home-range, predation risk can vary across food patches but missed opportunity should always be constant. However, it is not always obvious whether an animal is active in a single or multiple habitats. Even if an individual forages in multiple habitats, estimates of food availability may differ from one to the other because of travel costs among habitats as was likely the case in our study. Olsson and Molokwu's (2007) results are therefore relevant only in cases where animals have a homogenous travel rate among patches within their home range. Assuming that animals forage optimally, it might be advantageous for them to travel to neighbouring habitats to sample in periods when food is scarce in their own habitat. Results from a previous study (Tremblay 2000) suggest that grey squirrels have a lower travel cost and this could be why individuals were able to sample more than one habitat type.

We did not consider metabolic cost as a potential factor producing variation in GUDs. The metabolic cost associated with a habitat is usually a consequence of variation in climatic variables such as wind and temperature. For example, a fall or rise in temperature can cause a higher demand in energy when the ambient temperature is located outside the animal's thermo-neutral zone (Druce et al. 2006). We were able to neglect the effect of metabolic costs on perception of relative habitat quality for the following reasons: First, since our study took place in summer

and early fall, recorded temperatures usually fell within, or fairly close, to the animals' thermo-neutral zones. The thermo-neutral zone for red squirrels is between 15 and 30 ° C (Pauls 1978), between 28.5 and 32 ° C for chipmunks (Wang and Hudson 1971) and the lowest temperature of the zone is 25 °C for grey squirrels (Ducharme 1989). When the ambient temperature falls below the animal's thermo neutral zone, it must spend more energy than at its basal metabolic rate to maintain its temperature (Kilpatrick 2003). However, at any point in time, habitats rarely differed in temperature by more than a few degrees (°C) and consequently the difference was not enough to consider a temperature effect which would explain differences in GUDs. We also assumed that the possible energetic costs due to temperature were negligible compared to the average energetic gain obtained from feeding in our feeders.

Foraging efficiencies

It is clear that differences between species in habitat exploitation through foraging efficiencies do not generate a coexistence mechanism as the grey squirrel was always the most, or one of the most, efficient species during the span of our study. It was also the case for a previous study conducted at the Morgan Arboretum (Saropoulos 1996).

What is surprising is that *T. hudsonicus* was the least efficient forager in the coniferous forest although it is known to have a preference for coniferous forests and a diet consisting primarily of seeds from conifer cones (Benhamou 1996; Vlasman & Fryxell 2002; Holloway et Malcolm 2006). Perhaps the red squirrels' very high GUDs and their absence at the feeders indicate that they already have enough food in the habitat and therefore do not require the food in our artificial patches.

Visual observations made in the conifer forest of some cone piles suggest that they might still have sufficient cone reserves from the previous year. On the other hand, the lack of data and high GUDs for red squirrels might be a result of a high predation risk; if an environment is exposed to predation, the animals will leave more food behind and as a consequence, the habitat will become richer. Then again, a predator may already be responsible for reducing the red squirrel population and therefore increasing the food availability in the habitat. Thus, the few remaining individuals would have a higher missed opportunity costs and consequently leave higher GUDs. This is plausible because we observed very few red squirrels at the Morgan Arboretum in comparison to other years (Guerra & Vickery 1998; Tremblay 2000). In addition, compared with previous years (Tremblay 2000), red squirrels did not demonstrate aggressive interference with other species in our filmed trials which might suggest that they do not need to defend their food resource since it is so abundant in the habitat.

Although we initially proposed a coexistence mechanism related to spatial differences in habitat types, temporal variation was revealed to be more important. There is a clear temporal trade-off between two species: *S. carolinensis* is more active in feeders (more present) and more efficient in feeders earlier in the season whereas *T. striatus* is more active (more present) and more efficient in feeders later in the season (end of summer/ early fall). This makes sense because it may be more important for *T. striatus* to gather resources at the end of summer/early fall in order to prepare for hibernation which usually lasts from the end of October to mid-April (Woods 1980). On the other hand, the grey squirrel will have access to resources during winter. The grey squirrel is also probably less present in our feeders later in the season because it is more attracted to the recently ripened walnuts. Both Guerra & Vickery (1998) and Saropoulos (1996) also detected a significant interaction

between species and temporal variation but for different seasons. Grey squirrels were more efficient foragers in winter and spring whereas chipmunks were more efficient in summer (Saropoulos 1996). Similarly, a comparison of chipmunks to red squirrels reveals that the latter were more efficient foragers during February and March (because chipmunks were hibernating) whereas chipmunks were more efficient over the spring and summer in a mixed forest. It is important to note that our study was conducted over a shorter period (summer/early fall) and the temporal trade-off revealed appears to work on a much smaller scale than already well-known seasonal trade-offs (e.g. hibernation of chipmunks during winter permitting full access to resources for the other species). Of course, other mechanisms of coexistence might also occur during other periods of the year.

Our study shows that Rieucau et al.'s (2009) patch-use model can be used not only to explore potential species coexistence mechanisms but also to evaluate habitat for restoration managers. As emphasised by Whelan and Jedlicka (2007), patch use methods should be used in addition to current tools such as surveys for population monitoring. This is especially important since density does not necessarily correlate with habitat quality. This can be a consequence of temporal variation in density due to seasons, variation in food source abundance or simply due to social interactions (Van Horne 1983).

Future studies need to add a measure of density or a measure of reproductive success (a fitness proxy) to draw a bigger picture of how species coexist in different habitat types. These studies should also include an experimental design that would allow the validation of the Rieucau et al. (2009) model comparing habitat quality between habitats within the same environment. This could be done by

experimentally modifying the importance of predation risk between two habitat types.

CONCLUSION GÉNÉRALE

Dans cette étude, nous avons testé la validité du modèle Rieucau et al. (2009) dans le but d'utiliser ses inférences pour explorer l'effet de la variation spatiale selon l'habitat sur les coûts d'approvisionnement dans un contexte de coexistence. Les résultats obtenus suite à des analyses de modèles mixtes démontrent que les animaux réagissent aux changements de leur environnement selon les prédictions du modèle, validant ainsi son utilité pour le deuxième volet. Les écureuils gris ont réagi à l'enrichissement de la plantation de noyers noirs en laissant des GUDs et des ΓGUDs plus élevées. Les tamias, pour lesquelles les noix de noyers ne sont pas une ressource profitable, ont laissé des GUDs et des ΓGUDs similaires avant et après l'enrichissement du milieu dévoilant qu'ils n'ont pas réagi aux changements.

Le risque de prédation est souvent considéré comme l'un des plus importants facteurs déterminant le comportement d'approvisionnement. Cependant, selon les inférences du modèle, l'écureuil gris ainsi que le tamia considèreraient le coût d'opportunités manquées dans leurs décisions. L'écureuil gris et le tamia perçoivent la forêt de feuillus comme ayant le coût d'opportunités manquées le plus élevé. Cependant, le tamia y percevrait aussi un plus grand risque de prédation. Cela est possible puisqu'une haute abondance de nourriture peut attirer plus d'individus et à leur tour ceux-ci sont susceptibles d'attirer plus de prédateurs (Olsson & Emma 2007). D'un autre côté, un risque de prédation élevé fera que les proies laisseront plus de nourriture et par conséquence, l'habitat sera plus riche. Les tamias semblent percevoir la forêt de conifères comme moins risquée et avec le moins de nourriture. En revanche, l'écureuil gris semble percevoir la plantation de noyers avec le moins de nourriture. Une explication possible est que la majorité des GUDs des

écureuils gris ont été laissés avant la fructification des noyers (habitat pauvre en ressource) car ils étaient moins intéressés à visiter nos mangeoires lorsque les noix de noyers étaient abondantes.

Ni la perception de la qualité d'habitat ni l'efficience d'approvisionnement dans la forêt de feuillus ainsi que dans la plantation de noyers n'a pu être estimé pour l'écureuil roux puisque les GUDs ont été laissé presque qu'exclusivement dans la forêt de conifères (bien que l'animal fut observé dans chacun des habitats au cours de l'étude). Plusieurs études ont démontrés que la forêt de conifères semble être l'habitat préféré pour l'écureuil roux (Woods 1980; Ransome et Sullivan 1997; Holloway et Malcolm 2006). Celui-ci possède une préférence pour les forêts de pins et de sapins où il peut s'alimenter de graines des cônes de conifères, une ressource préférée faisant parti de sa diète (Woods 1980, Holloway et Malcolm 2006). Cependant, nos résultats démontrent que les deux autres espèces de sciuridés s'avèrent plus efficients en termes d'approvisionnement dans cet habitat. Nous considérons tout de même probable qu'il y a sélection d'habitat de la part des écureuils roux pour la forêt coniférienne puisque son activité dans les mangeoires était nettement supérieure aux autres espèces en plus d'être supérieur à son activité dans les deux autres habitats. Finalement, des études antérieures suggèrent que l'écureuil roux peut persister par ses interactions agressives (Guerra et Vickery 1998 ; Tremblay 2000). Toutefois, nos vidéos n'ont révélé aucune interaction agressive de la part de cette espèce pour la durée de l'étude. Il est possible que les GUDs très élevés des écureuils roux et leur absence dans les mangeoires indiquent qu'ils ont assez de nourriture dans l'habitat et par conséquent ne nécessitent pas la nourriture présente dans nos mangeoires. En revanche, un risque de prédation élevé peut être responsable; si un environnement est exposé à la prédation, les animaux laisseront plus de nourriture et par conséquence, l'habitat va devenir plus

riche. Là encore, un prédateur peut-être déjà responsable de la réduction de la population de l'écureuil roux en augmentant ainsi la disponibilité de la nourriture dans l'habitat. Ainsi, les quelques individus restants auraient un coût d'opportunité manquée plus élevée et laissera de ce fait un GUD plus élevé. Cela pourrait être plausible parce que nous avons observé très peu l'écureuil roux à l'Arboretum Morgan par rapport aux autres années (Guerra & Vickery, 1998; Tremblay 2000).

Nous n'avons pas détecté un compromis évident entre les trois espèces (ni dans la préférence d'habitat, ni dans l'efficience d'approvisionnement) qui considérerait que la sélection d'habitat soit le mécanisme principal permettant leur coexistence. Bien qu'il y ait certaines différences entre les espèces dans leurs perceptions des coûts d'approvisionnement, le fait que l'écureuil gris semble être toujours une des espèces les plus efficiente dans chacun des habitats laisse croire qu'il y a des mécanismes autre que la sélection d'habitat qui facilitent la coexistence de ces espèces. Le mécanisme qui semble ressortir de l'étude est celui d'un compromis temporel entre le tamia et l'écureuil gris. L'activité des écureuils gris dans les mangeoires (nombre de visites) ainsi que leur efficience étaient significativement plus élevées dans la première moitié de l'étude tandis que l'activité et l'efficience des tamias étaient plus élevées dans la dernière moitié. Ce compromis temporel plutôt que spatial permettrait aux deux espèces un accès aux ressources alimentaires.

En résumé, les résultats ont démontré que le risque de prédation ainsi que la disponibilité de nourriture agissent de façon simultanée sur le comportement des animaux étudiés. Dans le contexte ponctuel de l'étude, nous avons démontré qu'un compromis à l'échelle temporelle semble plus important que le compromis spatial prédit. Il est par contre important de noter qu'il reste possible que d'autres

mécanismes prévalent à d'autres moments de l'année. Enfin, nos résultats ont contribué à valider le modèle de Rieucau et al. (2009) basé sur un système de supplémentation.

L'approche basée sur la théorie d'approvisionnement optimal utilisée dans cette étude pourrait servir à étudier de nombreuses autres espèces, notamment celles qui sont en danger, afin de protéger les habitats que celles-ci perçoivent comme étant de meilleure qualité par l'estimation de la préférence d'habitat à l'aide du modèle Rieucau et al. (2009) et où elles possèdent une plus grande efficience. Comme projets futurs, il serait intéressant de valider le modèle comparant des habitats à l'intérieur du même environnement et dans une variété d'espèces ou de taxons.

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